

Using Ecological Function to Develop Recovery Criteria for Depleted Species: Sea Otters and Kelp Forests in the Aleutian Archipelago

JAMES A. ESTES,* M. TIM TINKER,† AND JAMES L. BODKIN‡

*Department of Ecology and Evolutionary Biology, Center for Ocean Health, Long Marine Laboratory, University of California, Santa Cruz, CA 95060, U.S.A. email jestes@ucsc.edu

†U.S. Geological Survey, 100 Shaffer Road, Santa Cruz, CA 95060, U.S.A.

‡U.S. Geological Survey, Alaska Science Center, 4210 University Drive, Anchorage, AK 99508, U.S.A.

Abstract: *Recovery criteria for depleted species or populations normally are based on demographic measures, the goal being to maintain enough individuals over a sufficiently large area to assure a socially tolerable risk of future extinction. Such demographically based recovery criteria may be insufficient to restore the functional roles of strongly interacting species. We explored the idea of developing a recovery criterion for sea otters (*Enhydra lutris*) in the Aleutian archipelago on the basis of their keystone role in kelp forest ecosystems. We surveyed sea otters and rocky reef habitats at 34 island-time combinations. The system nearly always existed in either a kelp-dominated or deforested phase state, which was predictable from sea otter density. We used a resampling analysis of these data to show that the phase state at any particular island can be determined at 95% probability of correct classification with information from as few as six sites. When sea otter population status (and thus the phase state of the kelp forest) was allowed to vary randomly among islands, just 15 islands had to be sampled to estimate the true proportion that were kelp dominated (within 10%) with 90% confidence. We conclude that kelp forest phase state is a more appropriate, sensitive, and cost-effective measure of sea otter recovery than the more traditional demographically based metrics, and we suggest that similar approaches have broad potential utility in establishing recovery criteria for depleted populations of other functionally important species.*

Keywords: Alaska, interaction strength, kelp, phase state, recovery, sea otter, sea urchins

Utilización de la Función Ecológica para Desarrollar Criterios de Recuperación para Especies Disminuidas: Nutrias Marinas y Bosques de Algas en el Archipiélago Aleutiano

Resumen: *Los criterios para la recuperación de especies o poblaciones disminuidas generalmente se basan en medidas demográficas, con la meta de mantener suficientes individuos en un área suficientemente extensa para asegurar un riesgo de extinción futura socialmente tolerable. Tales criterios de recuperación basados en demografía pueden ser insuficientes para restaurar los papeles funcionales de especies con interacciones estrechas. Exploramos la idea de desarrollar un criterio de recuperación para nutrias marinas (*Enhydra lutris*) en el archipiélago Aleutiano con base en su papel clave en los ecosistemas de bosques de algas. Muestreamos nutrias marinas y hábitats arrecifales rocosos en 34 combinaciones isla-tiempo. El sistema casi siempre existió en una condición de estado dominado por algas o deforestado, lo cual era pronosticable a partir de la densidad de nutrias marinas. Usamos un análisis de remuestreo de estos datos para mostrar que la condición de estado en una isla particular puede ser determinada con un 95% de probabilidad de clasificación correcta con información de seis sitios. Cuando se permitió que el estatus de la población de nutrias marinas (y por*

lo tanto, la condición de estado del bosque de algas) variara aleatoriamente entre islas, solo se tuvieron que muestrear 15 islas para estimar la verdadera proporción que estaba dominada por algas (dentro de 10%) con una confianza de 90%. Concluimos que la condición de estado del bosque de algas es una medida más apropiada, sensible y rentable de la recuperación de nutrias marinas que las medidas más tradicionales basadas en demografía, y sugerimos que métodos similares tienen una amplia utilidad potencial para el establecimiento de criterios de recuperación de poblaciones disminuidas de otras especies funcionalmente importantes.

Palabras Clave: Alaska, condición de estado, erizos de mar, fuerza de interacción, nutria marina, recuperación

Introduction

The biodiversity crisis has led to various guidelines and strategies for recovering depleted species. Recovery criteria are commonly based on estimates or measures of population size, status, and viability. Such criteria can be as simple as the minimum number of individuals required to achieve an acceptably low probability of extinction over some sufficiently long period of time (Soulé 1987). Typically, though, they are more complex, including considerations of distribution and range, population age and sex structure, metapopulation structure and dynamics, genetic variability, unforeseen or anticipated future risks, and temporal trends in these various metrics (Morris & Doak 2002). Regardless of the details, the determinants for recovery in practice are nearly always demographic in nature.

Although demographic considerations are always necessary, alone they may be insufficient as recovery criteria, especially if the species is a “strong interactor” (sensu Paine 1992; Power et al. 1996) and if demographic recovery occurs at a population size below that required for the species’ functional role in the ecosystem to be realized. Species influence their ecosystems through such well-known processes as competition, predation, mutualism, and the alteration of physical habitat. These influences may be as strong in some cases as to alter landscapes and associated patterns of biodiversity. Species capable of exerting such ecosystem-level influences have been referred to as keystone (Paine 1969) and foundation species (Dayton 1972), ecosystem engineers (Jones et al. 1994), and various other monikers that imply functional importance. In the broader interests of biodiversity conservation, recovery criteria for functionally important species should not only assure demographic viability but also an “ecologically effective population size” (Soulé et al. 2003, 2005).

Establishing recovery criteria on the basis of ecological function (hereafter, ecological effectiveness) calls for information that is fundamentally different from that required by the more traditional demographic approach. The development of such criteria requires identification of the key interaction web pathways through which the species influences its associated ecosystem; an understanding of the functional relationship between these influences and the species’ population size; the estab-

lishment of a state or range of states of these influences that constitute recovery; and the development of a quantitative criterion for classifying a given region as recovered. Following the recent decline (Doroff et al. 2003; Estes et al. 2005) and listing under the U.S. Endangered Species Act (70 FR 46366, 8 September 2005) of sea otters (*Enhydra lutris*) in southwestern Alaska, our goal here was to develop a recovery criterion for the species and its associated ecosystem on the basis of ecological effectiveness.

The Sea Otter-Kelp Forest System

Sea otters have well-documented and widely known effects on coastal ecosystems. Sea otter predation limits the distribution and abundance of their benthic invertebrate prey (Lowry & Pearse 1973), including crustaceans, bivalves, gastropods, and, perhaps most importantly, herbivorous sea urchins. Otter-induced urchin reductions increase the distribution and abundance of kelp (Estes & Palmisano 1974), an indirect interaction that occurs throughout much of the sea otter’s range (e.g., Breen et al. 1982; Estes & Duggins 1995; Kvitek et al. 1998). Top-down forcing processes of this sort, known as trophic cascades (Paine 1980; Carpenter & Kitchell 1993), occur widely in nature (Pace et al. 1999; Schmitz et al. 2000; Terborgh & Estes 2010).

The trophic cascade induced by sea otters drives rocky reef ecosystems to one of the two distinctive phase states (sensu Hughes 1994; Steneck et al. 2003): kelp forests or sea urchin barrens. These phase states imply thresholds, or a nonlinear relationship between otter abundance and ecosystem structure. These particular phase states are discrete and dichotomous because the end points in the potential continuum of variation between a kelp forest and a sea urchin barren are stable equilibria, whereas the intermediate community configurations are not (Estes & Duggins 1995). Urchin barrens tend to be self-sustaining because sea urchins switch their foraging behavior from sessile sit-and-wait consumers of detrital fallout when kelp is abundant to mobile hunters of living plants when kelp is rare or absent (Harrold & Reed 1985; Konar & Estes 2003). In addition, kelp stands, once established, use wave surge and flexible kelp stipes to physically

repel marauding sea urchins (Konar 2000; Konar & Estes 2003).

The trophic cascade initiated by sea otters has numerous indirect effects on other species and ecosystem processes. For example, the surface tension exerted by kelp on the water column attenuates waves and coastal currents, which in turn promotes sediment deposition and reduces coastal erosion (Jackson 1984, 1997). Kelp forests are more productive than sea urchin barrens, fixing an estimated 3–4 times more inorganic carbon per unit area through photosynthesis (Duggins et al. 1989), which increases growth rates and population sizes of various consumer species (Duggins et al. 1989; Estes 1996; Estes et al. 2004). For instance, the rock greenling (*Hexagrammos lagocephalus*), a common fish of kelp forests in the central and western Aleutian Islands, are an order of magnitude more abundant in kelp forests than in sea urchin barrens (Reisewitz et al. 2005). The indirect effects of sea otter predation also influence the behavior and foraging ecology of other coastal marine wildlife (e.g., Glaucous Winged Gulls [*Larus glaucescens*], Irons et al. 1986; Bald Eagles [*Haliaeetus leucocephalus*], Anthony et al. 2008).

Approach

Because ecosystems are inherently complex and often even difficult to define, the first step in developing a recovery criterion on the basis of ecological effectiveness is settling on a metric, which in turn raises a number of associated questions. Wide-ranging species typically occur in multiple habitat types. Does one develop the recovery criterion on the basis of all these or a selected few? Should the recovery criterion be based on a simple ecosystem metric or a more complex one involving all or some combination of the known effects of the target species? If the effect of the target species on its ecosystem is a graded response, how does one choose a specific level of that effect as a recovery criterion? And finally, ecosystems respond to many interacting variables or drivers, including bottom-up and top-down forcing processes. How does one account for the inevitable spatial and temporal variation in the chosen ecosystem state variable that is independent of the target species' effect on that ecosystem?

Many of these questions and potential difficulties are resolved by focusing the recovery criterion on those interaction-web processes that are most closely linked with the target species—in this case sea otters and the sea urchin-kelp trophic cascade, or more specifically on the abundance of kelp and sea urchins in rocky reef habitats. There are a number of reasons for such a focus. First, rocky reefs are common throughout the sea otter's natural range. Second, kelps and sea urchins are easily

measured and monitored in these reef habitats. Third, although the abundance of kelps and sea urchins vary substantially within and among sites (Estes & Duggins 1995) and even at specific sites over time (Watson & Estes, unpublished data), the configuration of the ecosystem is nearly always defined by one or the other of the two phase states—kelp forests or urchin barrens. This phase-state dichotomy simplifies the task of defining a recovery criterion and decision making to answering a yes-or-no question: Has the ecosystem recovered to a kelp-dominated state? Fourth, the predominate phase state in outer-coast reef habitats varies in response to sea otter predation throughout and even well beyond the geographic range of the decline of sea otter populations in southwestern Alaska. Finally, a database on kelp and sea urchin abundance is available within and beyond the range of the decline, from which a monitoring program to define any future changes in ecosystem phase state can be established.

Methods

Measurements of kelp and sea urchin abundance in the Aleutian archipelago have been obtained from numerous islands and at various times since the mid-1980s (Table 1). The sampling protocol was as follows. Randomly chosen sample sites were established along the shorelines of each island, initially from the intersection of a grid superimposed over the island's perimeter and later through a GIS-based routine in ARC GIS to generate random point distributions along the 7-m depth contour. Sites were excluded that fell on sand or mud bottom habitats (uncommon in the Aleutians). Although samples have been obtained from a range of depths, the patterns across depths are generally similar (except at depths <1–2 m, where intense wave surge favors kelp assemblages, and >15–20 m, where light attenuation precludes the settlement and growth of kelps). Sampling for this analysis was conducted at a depth of 6–8 m. Three to 31 sites were measured per island, depending on weather and time restrictions.

Multiple samples of the benthic community were taken at each site by placing a 0.5 × 0.5 m square quadrat at randomly spaced intervals on the seafloor. Kelps were counted and for simplicity pooled across species. Up to 20 quadrats were sampled per site, as determined by constraints of scuba-diving bottom time. Sea urchins were counted and collected from successive quadrats until 200 individuals were obtained or 20 quadrats were sampled, whichever was achieved first. Sea urchin test diameters were measured to the nearest millimeter. An allometric function relating urchin wet mass to test diameter was developed so that urchin biomass density could be

Table 1. Summary of the data sets used to examine the relationship between sea otter density and sea urchin biomass in the Aleutian islands.

<i>Island</i>	<i>Year</i>	<i>Number of sites</i>	<i>Urchin biomass (g·0.25 m⁻²)</i>	<i>Density of kelp (stipes·0.25 m⁻²)</i>
Adak	1987	28	29.99	9.09
Adak	1997	27	258.34	0.97
Adak	1999	30	269.12	1.49
Adak	2000	28	310.6	1.59
Agattu	1993	3	70.11	2.93
Akutan	1994	12	53.51	11.85
Alaid	1987	9	371.07	2.24
Alaid	1994	8	324.85	1.59
Amchitka	1987	29	31.19	5.33
Amchitka	1999	31	454.81	0.36
Amchitka	2000	11	361.53	0.24
Anangula	1994	4	1.15	17.01
Attu	1987	9	208.8	1.83
Attu	1990	14	127.31	2.08
Attu	1993	15	59.83	4.75
Attu	2000	15	35.14	3
Bering	2006	19	31.65	3.76
Chuginadak	1994	12	450.01	0.79
Kiska	1993	11	30.57	18.51
Kiska	2000	20	581.89	1.61
Nizki	1987	7	561.93	1.19
Nizki	1994	7	249.99	3.34
Nizki	1997	7	245.33	4.36
Ogliuga	1994	4	211.89	1.01
Rat	1994	10	611.9	1.06
Seguam	1994	10	514.66	0.24
Shemya	1987	16	413.81	0.79
Shemya	1994	12	250.48	4.28
Shemya	1997	16	426.44	3.3
Tanaga Bay	1994	7	118.79	3.74
Tanaga, Hot Sp	1994	6	45.91	8.88
Umnak	1994	4	3.77	9.08
Unalaska	1994	12	4.73	25.25
Yunaska	1994	10	515.27	0.77

estimated from numerical density and population size structure (Estes & Duggins 1995).

Our intent in using these procedures was to obtain a representative view of reef community structure at islands with varying sea otter densities in the Aleutian archipelago. Early data from islands with (Adak and Amchitka) and without (Alaid, Nizki, and Shemya) sea otters have been analyzed and are reported in Estes and Duggins (1995). Additional data were obtained from these islands and 12 others that were sampled one or more times during the past two decades. These latter data are from islands at which the sea otter populations were in various stages of recovery or decline when they were sampled. Altogether, the data were obtained between 1987 and 2006, during which time 34 island-by-year combinations (Table 1) have been sampled. Average urchin biomass and kelp densities were computed for each of these 34 island-year combinations.

We used *K*-means cluster analysis (Jain & Dubes 1988) to determine intrinsic groupings of the data and to assign each island × time data point to one of the identified groups. We then used linear discriminant analysis to as-

sess the effectiveness of the classification scheme and to create a canonical discriminant function that could be used to assign future data points to one cluster (ecosystem state) or the other.

We used a logistic regression to describe the relationship between ecosystem state (a categorical response variable defined as 0 [deforested] or 1 [kelp dominated]) and sea otter density (number of animals counted per kilometer surveyed). This analysis was restricted to island-year combinations for which we had both benthic survey data and counts of sea otters taken from skiffs ($n = 17$).

We next applied a bootstrapped resampling analysis to the full database ($n = 463$ sites at 34 island-year combinations, 10,000 iterations per sampling scenario) to determine the probability of assigning islands to their correct ecosystem phase states with varying numbers of sample sites per island. Because population recovery of sea otters may occur asynchronously among islands, we expanded this analysis to determine the number of islands that must be sampled to be reasonably sure that the majority (i.e., >50%) were either dominated by kelp or deforested. We conducted this expanded analysis to

estimate the true proportion of recovered islands (within 10%) with >95% accuracy. We selected a 50% threshold value as the least arbitrary criterion for large-scale ecosystem recovery (short of requiring recovery at every island, in which case the necessary sampling effort would be less).

Results

Information on kelp density and urchin biomass collected in 1987 from five islands in the Aleutian archipelago at which sea otters were either at or near carrying capacity (Adak and Amchitka) or absent (Alaid, Nizki, and Shemya) sorted into largely nonoverlapping areas of the two-dimensional phase space (see Fig. 7 in Estes & Dugins 1995). Islands with abundant sea otters consistently had low urchin biomass densities and high but variable kelp densities. Islands lacking sea otters, in contrast, consistently had low kelp densities and high but variable urchin biomass densities. These findings established that the rocky reef ecosystem structure (i.e., phase state) in the Aleutian Islands is predictable depending on the presence or absence of sea otters.

The remaining data sets aggregated similarly, which indicated the rarity or absence of intermediate community configurations associated with phase-state transformations. This pattern held regardless of whether the data were averaged by sites (Fig. 1a) or by islands (Fig. 1b). The tendency for each island-year combination of the data to sort into one of two distinct groups (K-means cluster analysis, Fig. 2) that corresponded to the alternate phase states was highly robust (discriminant analysis, jackknife classification accuracy = 100%, $F_{2,31} = 44.644$, $p < 0.001$). The linear canonical discriminant function ($df = -1.8391 + 0.0087 \times \text{urchin biomass density} - 0.0593 \times \text{kelp density}$) is thus a reliable algorithm for assigning any future data to the appropriate ecosystem phase state. If $df > -0.295$, the ecosystem state should be classified as urchin dominated; otherwise, the ecosystem state should be classified as kelp dominated. The threshold estimate of sea otter abundance required to affect the phase shift was 6.3/km of coastline (Fig. 3).

The optimal sample sizes (number of sites per island and number of islands) required to detect the ecosystem phase state depends largely on the geographic pattern of sea otter decline and recovery. Under the simplest scenario—that the entire archipelago is in one phase state or the other (approximately the current situation)—six sites from any island (or combination of islands) would be sufficient to provide a 95% probability of correct classification (Fig. 4a). Additional islands would have to be sampled if the various islands recovered at different times (as might be expected, for example, if recovery occurred through outgrowth from one or several remnant colonies). Under this latter scenario the optimal sampling

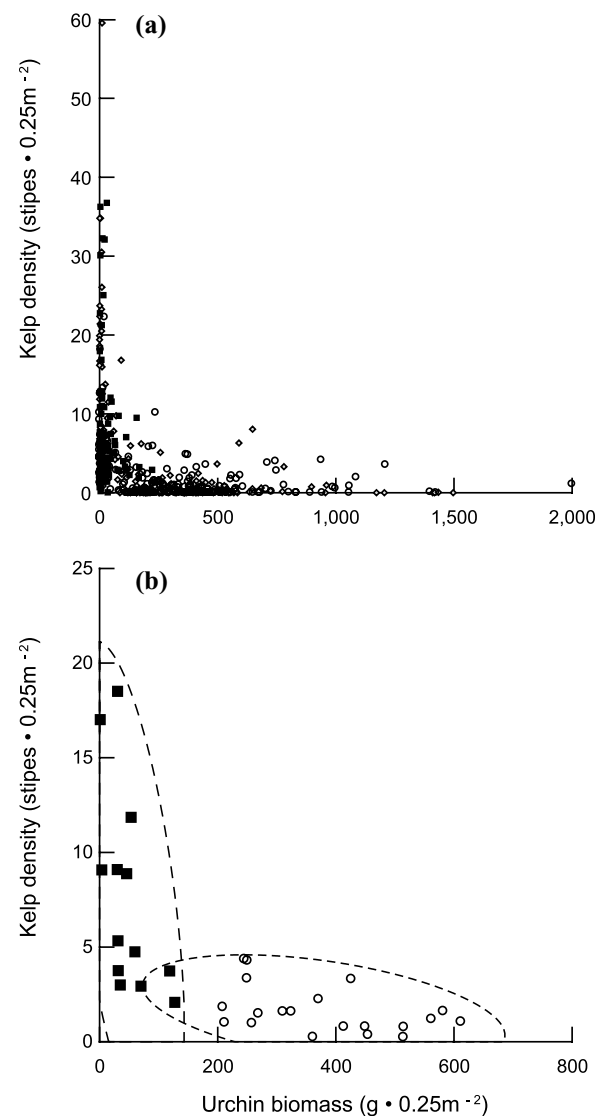


Figure 1. (a) Kelp density versus urchin biomass from the Aleutian archipelago, measured at 463 sites from 19 islands between 1987 and 2006: open circles, sites with low-density populations of sea otters (<6 otters/km surveyed); solid squares, sites with high-density populations (>6 otters/km surveyed); grey-shaded diamonds, sites where abundance of sea otters was not measured. (b) Data from (a) averaged by island-year combination. Dashed lines are 90% confidence ellipses around the two aggregates identified by K-means cluster analysis, which reflect the kelp-dominated (solid squares) and urchin-dominated (open circles) phase states. Each data point represents the average of all sites sampled at one island during 1 year ($n = 34$ island-year combinations).

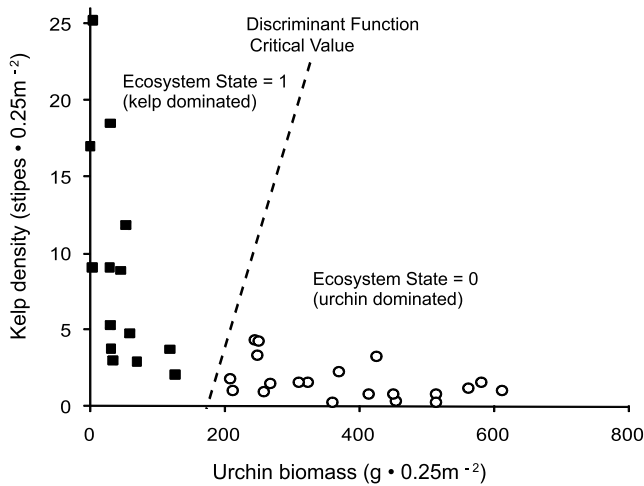


Figure 2. Results of a canonical discriminant analysis of subtidal sampling data from 34 island-year combinations (Table 1) that were classified by K-means cluster analysis into one of two ecosystem phase states: urchin dominated (open circles) or kelp dominated (solid squares).

strategy will vary depending on the geographic pattern of recovery and the proportion of islands in each of the two phase states. The most problematic situation (in terms of statistical power) will occur when islands recover randomly and asynchronously and one wishes to know that at least half of them have attained the kelp-dominated phase state. In this case, 23 islands must be sampled to provide a 95% probability of correctly estimating the true

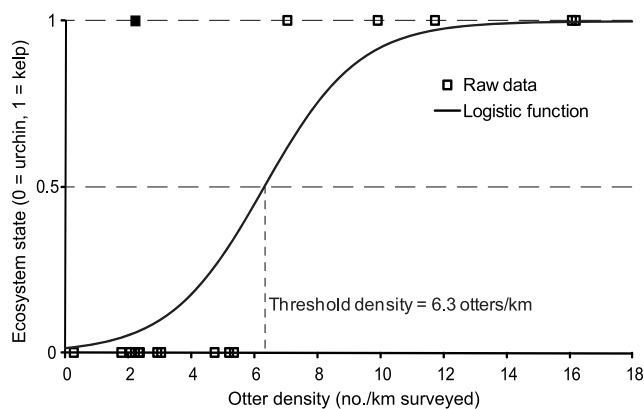


Figure 3. Logistic regression of ecosystem phase state versus sea otter density (from skiff-based surveys) estimated with data from 17 island-year combinations (open symbols). The one anomalous data point (Attu Island, 2000; solid symbol) is explained by the fact that all of the diving surveys that year were carried out in Massacre Bay because of inclement weather and the short time window available for sampling.

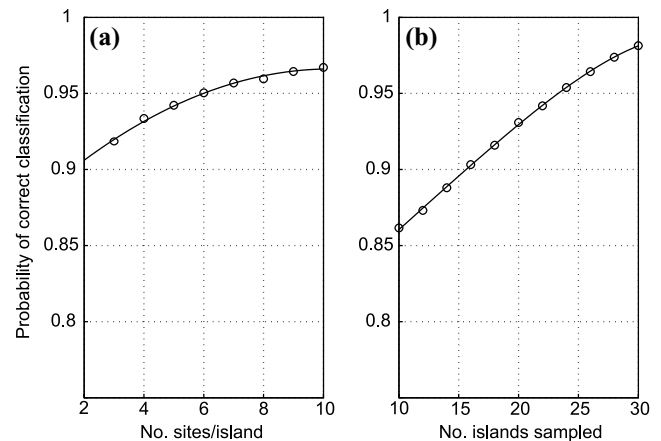


Figure 4. Sampling intensity versus statistical power to correctly classify ecosystem phase state: (a) probability of correctly classifying an island into one phase state or the other as a function of the number of sites sampled and (b) probability of correctly estimating the proportion of islands in the Aleutian archipelago in a given phase state (within 10% and assuming the actual proportion was 50%) as a function of the number of islands sampled.

proportion within 10%, or 15 islands must be sampled when the probability is relaxed to 90% (Fig. 4).

Discussion

Use of the rocky-reef phase state as a recovery criterion for sea otters in the Aleutian Islands offers several advantages over standard demographic approaches. One is that the abundance and distribution of the key organisms (kelps and sea urchins), both enormously more abundant and less mobile than sea otters, are far easier and more efficient to sample. This results in relatively small sampling error and thus greater statistical power to detect change. Another advantage is that because ecosystem phase state is a discrete variable, whereas sea otter abundance is a continuous variable, a recovery criterion derived from phase state can be determined more simply and objectively than one derived from sea otter demography. Another benefit of the approach is that it expands the criterion for recovery from demographic minimalism to ecological effectiveness, as urged by Soulé et al. (2003, 2005). We are not arguing that direct measures of sea otter demography be forsaken in favor of those pertaining to ecological effectiveness. Rather, we believe the inclusion of a measure of ecological effectiveness makes the recovery criterion more powerful, more objective, more relevant to biodiversity, and thus more useful to management and conservation.

Our assertion is that sea otters in the Aleutian Islands should not be delisted as threatened under the U.S. Endangered Species Act until an ecosystem phase shift to the kelp-dominated state has been achieved. If one accepts this assertion, then it becomes important to know what sort of field-monitoring effort would be required to establish the ecosystem's phase state with a sufficiently high level of statistical confidence to serve as a recovery criterion. The nonoverlapping 90% confidence ellipses around measures of sea urchin and kelp abundance from islands with varying densities of sea otters (Fig. 1b) showed this is a straight-forward undertaking, and the canonical discriminant function fit to these data (Fig. 2) provided a precise algorithm for assigning any future data that might be gathered to the appropriate phase state. The cluster analysis indicated little or no ambiguity in assigning islands to phase states with as few as three sites sampled per island (Fig. 1b). An independent resampling analysis supported this view because it showed that only six sample sites from a given island were sufficient to determine the ecosystem phase state with 95% certainty (Fig. 4a).

The determination of how many islands to sample was more complicated. Under a scenario of phase-state uniformity throughout the Aleutian archipelago, samples from just one island were adequate to characterize the region. This is probably more or less the current situation (Estes et al. 2004; B. Konar and J.A.E., unpublished data) due to the collapse of sea otters over that entire area (Doroff et al. 2003). Nevertheless, spatial (i.e., interisland) variability in phase state, as might occur if populations of sea otters declined or recovered in a temporally asynchronous manner, requires the sampling of multiple islands. Under this situation it becomes important to decide on the proportion of the islands (or area) that must be in the kelp phase state to constitute recovery and to know how many islands one must sample to make that determination. If the proportion of kelp-dominated islands is near zero or one, the precision of the estimate is unimportant and a small number of islands would suffice. If, on the other hand, the proportion is near 0.5, then a relatively large number of islands must be sampled to determine, with a reasonable degree of confidence, whether that proportion is greater or less than 0.5. The resample analysis for this latter situation indicated that 15 islands must be sampled to estimate the true proportion of kelp-dominated islands within approximately 10% with <10% chance of error. Given that six sites can be sampled easily by two or three dive teams in a single day, such a sampling effort would require 15 days of ship time, although ship-support time could be halved (to 8 days) by sampling two or more nearby islands in 1 day.

The preceding scenario is founded on the assumption that islands with different phase states occur randomly across the archipelago, an unlikely situation. Among-island variation in phase state probably would occur in a

more aggregated manner, in which case many fewer islands would need to be sampled. A monitoring program in which six sites are sampled from five to seven islands distributed more or less uniformly across the archipelago is probably more than sufficient for future decision making. This level of monitoring could be accomplished easily in a 2-week cruise.

The power in our proposed approach derives from the fact that rocky-reef phase states in the Aleutian archipelago are geographically extensive and highly predictable consequences of sea otter predation. Furthermore, the use of ecosystem phase states as a recovery criterion probably offers a more precautionary approach to recovery than one derived solely from viable population considerations because relatively high sea otter densities are required to drive the system from the urchin- to kelp-dominated phase state in the Aleutian Islands (Estes & Duggins 1995; Soulé et al. 2003).

The cost differential between population and ecosystem-based monitoring in this particular case is also substantial. For example, the aircraft charter for an aerial survey of sea otters in the Aleutians conducted in 2000 by the U.S. Fish and Wildlife Service cost approximately US\$250,000, an effort that provided no formal estimates of bias or precision. The cost of a reliable population assessment would be further increased because a time series of counts is needed to establish population trends with reasonable statistical confidence. Assuming a vessel charter cost of US\$6000 per day (roughly the current rate) and that 2 weeks of ship time would be required to conduct an archipelago-wide reef survey, the field support costs for assessing whether or not sea otters had reached an ecologically effective population size across the Aleutian archipelago would be about three times less than those for just one aerial survey of this same region.

We reiterate that we are not advocating that monitoring of population trends be forgone entirely in favor of ecosystem-based monitoring: the former are still required to ensure that demographic viability is achieved, and knowledge of the direction of population trends will be useful in interpreting changes in community state (and vice versa). In the Aleutians, skiff-based surveys of sea otters could be conducted simultaneously with an archipelago-wide reef survey for little extra cost.

Different conditions and ecological responses will apply in other parts of the sea otter's range. Phase-state transitions from urchin barrens to kelp forests occur more rapidly and at lower sea otter densities in southeastern Alaska (Estes & Duggins 1995), and reef systems along the southern coast of the Alaska Peninsula (authors' unpublished data) and Prince William Sound (Dean et al. 2000) persist in the kelp-dominated phase state even after reductions of sea otter populations to densities that would cause a phase shift in the Aleutian Islands. These differing functional relationships probably relate to differing regional patterns of sea urchin

recruitment (Estes & Duggins 1995). In California the spatial patterns of phase-state distributions are different still, with extensive kelp forests persisting amidst similarly extensive deforested areas in habitats devoid of sea otters (Foster & Schiel 1988). Despite this regional variation, sea otters exert strong and easily measurable environmental effects wherever they occur. Our proposed approach should thus be applicable, with appropriate adjustments, in any particular place.

Ecological influences will vary among species and across ecosystems, depending on the pathways a species' direct effects follow as they spread through the interaction web. The concept of ecological effectiveness, however, is not limited to strong interactors because the loss of both strong and weak interactors can destabilize complex food webs (O'Gorman & Emmerson 2009). An ecologically based recovery criterion may not be necessary for all species. Nevertheless, the ecological roles of most species are poorly understood; hence, the precautionary approach in developing recovery strategies is to assume they are functionally important until shown otherwise.

Broadly similar approaches to the one we propose for sea otters and kelp forests should be applicable to any ecosystem within which depleted species are functionally important and the relationship between the target species' abundance and ecosystem response is sufficiently well known or can be determined. For example, measurements of vegetation might provide a useful adjunct to population assessments in determining whether or not gray wolves (*Canis lupus*) should be considered recovered in the Greater Yellowstone Ecosystem because wolves prey on elk (*Cervus canadensis*) and other large ungulates, which in turn reduces the impacts of browsing on various woody plants (Ripple & Beschta 2003, 2006). Similarly, populations of bivalve mollusks and even water clarity might help in assessing the degree to which great shark populations have recovered from overexploitation in east-coast estuaries of the United States because great shark population declines have led to small elasmobranch (small sharks, skates, and rays) population eruptions, which depresses populations of filter-feeding bivalves (Myers et al. 2007) and leads in turn to reduced water clarity (Jackson et al. 2001; Lotze et al. 2006). In both cases, the suggested metrics would be easier to observe (and possibly even easier to interpret) than assessments of the distribution, abundance, and population trends of the apex predators themselves.

The assessment of ecological effectiveness for sea otters and kelp forests is simplified by the discrete nature of the forested and deforested phase states. Whether such keystone influences in other systems lead to discrete phase states or graded responses remains uncertain, although nonlinear dynamics and multiple stable states are likely common in nature (Scheffer 2009). The larger challenge is twofold—understanding the ecological importance of species (Kareiva & Levin 2004) and

then applying this understanding to the establishment of appropriate functionally based recovery criteria. Meeting this challenge will force a shift in attention from species to ecosystems in the management and conservation of living resources, a goal with more solid ecological grounding and broader utility than the often arbitrary numerical criteria attached to single species.

Acknowledgments

The impetus for this work arose during our participation on the U.S. Fish and Wildlife Service's southwest Alaska Sea Otter Recovery Team. We thank C. Eisenberg, M. Soulé, and various members of the southwest Alaska sea otter Recovery Team for discussions and comments on earlier drafts of the manuscript. Evaluations by L. Gerber and two anonymous referees led to further improvements. Funding for the field work over the years was provided by grants from the National Science Foundation, a contract from the U.S. Navy, and base research support from the U.S. Geological Survey. We are especially grateful to the Alaska Maritime National Wildlife Refuge for their long standing interest in our work and the logistical support for our research in the Aleutian Islands.

Literature Cited

- Anthony, R. G., J. A. Estes, M. A. Ricca, A. K. Miles, and E. D. Forsman. 2008. Bald eagles and sea otters in the Aleutian archipelago: indirect effects of trophic cascades. *Ecology* **89**:2725–2735.
- Breen, P. A., T. A. Carson, J. B. Foster, and E. A. Stewart. 1982. Changes in subtidal community structure associated with British Columbia sea otter transplants. *Marine Ecology Progress Series* **7**:13–20.
- Carpenter, S. R., and J. F. Kitchell. 1993. *The trophic cascade in lakes*. Cambridge University Press, New York.
- Dayton, P. K. 1972. Toward an understanding of community resilience and the potential effects of enrichment to the benthos at McMurdo Sound, Antarctica. Pages 81–96 in B. C. Parker, editor. *Proceedings of the Colloquium on conservation problems in Antarctica*. Allen Press, Lawrence, Kansas.
- Dean, T. A., J. L. Bodkin, S. C. Jewett, D. H. Monson, and D. Jung. 2000. Changes in sea urchins and kelp following a reduction in sea otter density as a result of the *Exxon Valdez* oil spill. *Marine Ecology Progress Series* **199**:281–291.
- Doroff, A. M., J. A. Estes, M. T. Tinker, D. M. Burn, and T. J. Evans. 2003. Sea otter population declines in the Aleutian archipelago. *Journal of Mammalogy* **84**:55–64.
- Duggins, D. O., C. A. Simenstad, and J. A. Estes. 1989. Magnification of secondary production by kelp detritus in coastal marine ecosystems. *Science* **245**:170–173.
- Estes, J. A. 1996. The influence of large, mobile predators in aquatic food webs: examples from sea otters and kelp forests. Pages 65–72 in S. P. R. Greenstreet and M. L. Tasker, editors. *Aquatic predators and their prey*. Fishing News Books, Oxford, United Kingdom.
- Estes, J. A., M. T. Tinker, A. M. Doroff, and D. Burn. 2005. Continuing decline of sea otter populations in the Aleutian archipelago. *Marine Mammal Science* **21**:169–172.
- Estes, J. A., E. M. Danner, D. F. Doak, B. Konar, A. M. Springer, P. D. Steinberg, M. T. Tinker, and T. M. Williams. 2004. Complex trophic interactions in kelp forest ecosystems. *Bulletin of Marine Sciences* **74**:621–638.

- Estes, J. A., and J. F. Palmisano. 1974. Sea otters: their role in structuring nearshore communities. *Science* **185**:1058–1060.
- Estes, J. A., and D. O. Duggins. 1995. Sea otters and kelp forests in Alaska: generality and variation in a community ecological paradigm. *Ecological Monographs* **65**:75–100.
- Foster, M. S., and D. R. Schiel. 1988. Kelp communities and sea otters: keystone species or just another brick in the wall? Pages 92–115 in G. R. Van Blaricom and J. A. Estes, editors. *The community ecology of sea otters*. Springer-Verlag, Berlin.
- Harrold, C., and D. C. Reed. 1985. Food availability, sea urchin grazing, and kelp forest community structure. *Ecology* **66**:1160–1169.
- Hughes, T. P. 1994. Catastrophes, phase shifts, and large-scale degradation of a Caribbean coral reef. *Science* **265**:1547–1551.
- Irons, D. B., R. G. Anthony, and J. A. Estes. 1986. Foraging strategies of Glaucous-winged Gulls in rocky intertidal communities. *Ecology* **67**:1460–1474.
- Jackson, G. A. 1984. Internal wave attenuation by coastal kelp stands. *Journal of Physical Oceanography* **14**:1300–1306.
- Jackson, G. A. 1997. Currents in the high drag environment of a coastal kelp stand off California. *Continental Shelf Research* **17**:1913–1928.
- Jackson, J. B. C., et al. 2001. Historical overfishing and the recent collapse of coastal ecosystems. *Science* **293**:629–638.
- Jain, A. K., and R. C. Dubes. 1988. *Algorithms for clustering data*. Prentice Hall, Englewood Cliffs, New Jersey.
- Jones, C. G., J. H. Lawton, and M. Shachak. 1994. Organisms as ecosystem engineers. *Oikos* **69**:373–386.
- Kareiva, P., and S. A. Levin, editors. 2004. *The importance of species*. Princeton University Press, Princeton, New Jersey.
- Konar, B. 2000. Seasonal inhibitory effects of marine plants on sea urchins: structuring communities the algal way. *Oecologia* **125**:208–217.
- Konar, B., and J. A. Estes. 2003. The stability of boundary regions between kelp beds and deforested areas. *Ecology* **84**:174–185.
- Kvitek, R. G., P. Iampietro, and C. E. Bowlby. 1998. Sea otters and benthic prey communities: a direct test of the sea otter as keystone predator in Washington State. *Marine Mammal Science* **14**:895–902.
- Lotze, H. K., H. S. Lenihan, B. J. Bourque, R. Bradbury, R. G. Cooke, M. C. Kay, S. M. Kidwell, M. X. Kirby, C. H. Peterson, and J. B. C. Jackson. 2006. Depletion, degradation and recovery potential of estuaries and coastal seas. *Science* **312**:1806–1809.
- Lowry, L. F., and J. S. Pearse. 1973. Abalones and sea urchins in an area inhabited by sea otters. *Marine Biology* **23**:213–219.
- Morris, W., and D. F. Doak. 2002. *Quantitative conservation biology: theory and practice of population viability analysis*. Sinauer Associates, Sunderland, Massachusetts.
- Myers, R. A., J. K. Baum, T. D. Shepherd, S. P. Powers, and C. H. Peterson. 2007. Cascading effects of the loss of apex predatory sharks from a coastal ocean. *Science* **315**:1846–1850.
- O’Gorman, E. J., and M. C. Emmerson. 2009. Perturbations to trophic interactions and the stability of complex food webs. *Proceedings of the National Academy of Sciences* **106**:13393–13398.
- Pace, M. L., J. J. Cole, S. R. Carpenter, and J. F. Kitchell. 1999. Trophic cascades revealed in diverse ecosystems. *Trends in Ecology Evolution* **14**:483–488.
- Paine, R. T. 1969. A note on trophic complexity and species diversity. *The American Naturalist* **103**:91–93.
- Paine, R. T. 1980. Food webs: linkage, interaction strength and community infrastructure. *Journal of Animal Ecology* **49**:667–685.
- Paine, R. T. 1992. Food-web analysis through field measurement of per capita interaction strength. *Nature* **355**:73–75.
- Power, M. E., D. Tilman, J. A. Estes, B. A. Menge, W. J. Bond, L. S. Mills, G. Daily, J. C. Castilla, J. Lubchenco, and R. T. Paine. 1996. Challenges in the quest for keystones. *BioScience* **46**:609–620.
- Reisewitz, S. E., J. A. Estes, and S. A. Simenstad. 2005. Indirect food web interactions: sea otters and kelp forest fishes in the Aleutian archipelago. *Oecologia* **146**:623–631.
- Ripple W. J., and R. L. Beschta. 2003. Wolf reintroduction, predation risk, and cottonwood recovery in Yellowstone National Park. *Forest Ecology and Management* **184**:299–313.
- Ripple W. J., and R. L. Beschta. 2006. Linking wolves to willows via risk-sensitive foraging by ungulates in the northern Yellowstone ecosystem. *Forest Ecology and Management* **230**:96–106.
- Scheffer M. 2009. *Critical transitions in nature and society*. Princeton University Press, Princeton, New Jersey.
- Schmitz, O. J., P. A. Hambäck, and A. P. Beckerman. 2000. Trophic cascades in terrestrial systems: a review of the effects of carnivore removals on plants. *The American Naturalist* **155**:141–153.
- Soulé, M. E. 1987. *Viable populations for conservation*. Cambridge University Press, Cambridge, United Kingdom.
- Soulé, M. E., J. A. Estes, J. Berger, and C. Martinez del Rio. 2003. Recovery goals for ecologically effective numbers of endangered keystone species. *Conservation Biology* **17**:1238–1250.
- Soulé, M. E., J. A. Estes, B. Miller, and D. A. Honnold. 2005. Strongly interacting species: conservation policy, management, and ethics. *BioScience* **55**:168–176.
- Steneck, R. S., M. H. Graham, B. J. Bourque, D. Corbett, J. M. Erlandson, J. A. Estes, and M. J. Tegner. 2003. Kelp forest ecosystem: biodiversity, stability, resilience and future. *Environmental Conservation* **29**:436–459.
- Terborgh, J., and J. A. Estes, editors. 2010. *Trophic cascades: predators, prey, and the changing dynamics of nature*. Island Press, Washington, D.C. (in press).